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The goal of this investigation was to understand the neural computations that mediate the precision of human spatial vision. We approached this goal along three interrelated lines of research: 1) direct investigation of human and monkey retinal sampling mosaics; 2) psychophysical measurements of the precision of human spatial vision; and 3) computer simulations of human visual processes based on "biologically correct" sampling lattices and "behaviorally constrained" neural models of human spatial information processing. Our progress is described in the following report.

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A. SPECIFIC AIMS OF RESEARCH PROJECT:

The long term goal of our research program is to understand the neural computations that mediate the precision of human spatial vision. We approach this goal with three interrelated lines of research: 1) direct investigations of human and monkey retinal sampling mosaics; 2) psychophysical measurements of the precision of human spatial vision; and 3) computer simulations of human visual processing based on "biologically correct" sampling lattices and "behaviorally constrained" neural networks of human spatial information processing. Quantification of the anatomical sampling lattices provides a novel technique to understand how the physical structures influence the neural represention of the spatial information contained in the original image. The psychophysical data serve to "calibrate" the human spatial vision system and to guide the develoment of computer simulations. The computer simulations provide biological insight into the neural basis of spatial vision. Following are the three specific aims addressed in this research project:

A1. Characterize the human and monkey photoreceptor sampling lattice and relate the findings to limits of spatial vision;

A2. Investigate new spatial discriminations in two-dimensions such as circle center, area, and random dot discriminations and relate to distributed models of spatial vision;

A3. Develope a new system of computer simulations to evaluate the biological consequences of sampling and specific models of spatial processing.

B. REPORT ON SPECIFIC AIM 1:

B1. List of publications:

B1a. Hirsch, J. and Curcio, C.A. The spatial resolution capacity of human foveal retina. Vision Res., 29, 1095-1101, 1989.

B1b. Samy, C.N. and Hirsch, J. Differences between human and monkey retinal sampling mosaics suggest a strategy that enhances human visual sensitivity and resolution. Visual Neuroscience, 3, 281-285, 1989.

B1c. Hirsch, J. and Miller, Wm. H. Does cone positional disorder limit near-foveal acuity? J. Opt. Soc. Am. A., 4, 1481-1492, 1987.

B1d. Samy, C.N. and Hirsch, J. Comparison of human and monkey retinal photoreceptor sampling mosaics. Yale Journal of Biology and Medicine, 63, In press, 1990.

B1e. Hirsch, J. and Samy, C.N. Human and monkey photoreceptor lattices are fundamentally similar but not completely isomorphic. Supplement to Investigative Ophthalmology and Visual Science, 29, 58, 1988.

B1f. Hirsch, J. and Curcio, C. A. Sampling by the human retina predicts grating resolution within 2.0°. Opt. Soc. of Am. Technical Digest Series, 22, 83, 1987.

B1g. Hirsch, J. and Miller, W.H. The sampling theorem overestimates acuity beyond 1.25 degrees of eccentricity. Supplement to Investigative Ophthalmology and Visual Science, 28, 360, 1987.

B2. Summary of main findings

B2a. Anatomical resolving power and human acuity

An image on the retina of a human eye enters the visual system through an array of photoreceptors that sets the boundaries on the spatial detail available for nerual representation. In order to investigate the extent to which the input spatial detail is preserved by the human neural system, we compare the anatomical spatial limits as determined by the Nyquist frequency, the highest spatial-frequency reconstructable from the cone array, and measures of human acuity, the minimum angle resolvable. We find that the anatomical Nyquist limits determined along the temporal horizontal meridiam of a well-studied human retina (Curcio, Sloan, Packer, Hendrickson & Kalina, 1987) offer a reasonable prediction of human acuity within the retinal region extending from slightly off the foveal center to about 2.0 deg of retinal eccentricity. However, we find a narrow peak of anatomical resolution at the foveal center where the acuity appears to be overestimated by cone spacing. (Refs: B1a and B1f)

B2b. Cone positional disorder and limits of visual resolution

We measure the center-to-center spacings and disorder is spacings beween all pairs of cones in a strip of primate retina extending from the foveal center to approximately 5.75 deg of retinal eccentricity along the temporal horizontal meridiam. The strip is partitioned into windows, and the positions of the cone centers in each lattice window are digitized for analysis of lattice structure and quality. We find a nearly monotonic increase in cone spacing and eccentricity. The cone mosaic is a high-quality hexagonal lattice near the foveal center, and the cone positional disorder (jitter) relative to average spacing increases beyond 1.5 deg. We estimate human acuity measures through the optics of eyes over a retinal region comparable to our lattice strip by pooling the results of previous investigators. When the monkey lattice is scaled to human foveal resolution, application of the sampling theorem to average cone spacing predicts these pooled visual-acuity data from the foveal center to about 1.5 deg and overestimates visual acuity more eccentically. We conclude that the sampling theorem based on average spacing overestimates the pooled estimate of visual acuity from the foveal edge to about 5 deg, probably because of sampling noise caused by orientation and spacing disorder combined with demodulation as a result of the optics of the eye. (Refs: B1c and B1g)

B2c. Comparision of human and monkey foveal sampling lattices

We test the hypothesis that the diameters of foveal and near-foveal rods and cones for one well-studied human photoreceptor mosaic (H4 of Curcio, et al, 1987) and one well-studied monkey photoreceptor mosaic (Macaca fascicularis of Hirsch and Miller, 1987) are scaled relative to focal length. We conclude that this hypothesis is not supported. Rather than being scaled proportionally, the sizes of the rods and cones respectively are nearly equivalent for both the human and monkey resulting in an effectively finer retinal grain for the larger human eye. Furthermore, the human rod density exceeds the monkey rod density beyond about 1 degree of retinal eccentricity. These results suggest that variation across primate species is reflected in retinal sampling strategies. (Refs: B1b and B1e)

C. REPORT OF SPECIFIC AIM 2:

C1. List of publications

C1a. Hirsch, J. and Mjolsness, E. A center-of-mass computation describes the precision of random dot displacement discrimination. Submitted, 1990.

C1b. Hirsch, J. and Groll, S.L. The precision of separation discrimination can be enhanced by orientation features. Submitted, 1990.

C1c. Groll, S.L. and Hirsch, J. Two-dot vernier discrimination within 2.0 degrees of retinal fovea. J. Opt. Soc. Am. A., 4, 1535-1542, 1987.

C1d. Hirsch, J. and Mjolsness, E. Evidence for spatial discrimination based on global variables. Supplement to Investigative Ophthalmology and Visual Science, 30, 454, 1989.

C1e. Groll, S.L. and Hirsch, J. Circle size discrimination obey's Weber's Law and also exceeds separation discrimination for comparable stimuli. Supplement to Investigative Ophthalmology and Visual Science, 29, 448, 1988.

C1f. Gallant, J.L. and Hirsch, J. Masking reduces separation and spatial-frequency discrimination more at larger than smaller spacing. Supplement to Investigative Ophthalmology and Visual Science, 28, 360, 1987.

C1g. Hirsch, J. and Groll, S.L. Discrimination of the center position of a circle exceeds discrimination of the center position between two dots for stimuli beyond a critical size. Technical Digest, Optical Society of Am., 111, 1986.

C1g. Groll, S.L. and Hirsch, J. The Weber fraction for vernier discrimination increases between the fovea and approximately 2 degrees of retinal eccentricity and levels off from 2 to 5 degrees. Supplement to Investigative Ophthalomology and Visual Science, 27, 341, 1986.

C2. Summary of main findings

C2a. A new paradigm: Discrimination of dot displacements in random dot arrays

We test three models of how the human visual system computes a just-noticable-difference, jnd, in spatial separation using a new discrimination task that measures the precision with which displacements of random dots in random dot arrays can be detected. Fits of these models to the data convincingly exclude the two models where the displacement discrimination is based on either point-to-point or bin-to-bin measurements of local dot positions. However, the data are consistent with a model where displacement discrimination is based on a globally computed center-of-mass parameter. This finding enlarges the current view of spatial discriminaion models to include the effects of previously unexplored complex spatial variables such as stimulus complexity (number of dots) and multiplicity (number of dots displaced) on the precision of displacement discriminations.(Refs: C1a and C1d)

C2b. Discrimination precision is enhanced by orientation features

We test the hypothesis that spatial separations govern the precision of spatial discriminations for two-dot, two-line, circle, and Vernier stimuli by comparing the fractional just-noticeable-difference, jnd, in separation, $\Delta s/s$, for each task

over comparable separations. We find that, although Weber's Law generally applies for each of these tasks, separation discrimination for dot pairs configured along imaginary parallel lines (one orientation) is not as accurate as the same dot pairs configured along the circumferences of imaginary circles (multiple orientations) over the same ranges of feature separations. Similarly, two-dot Vernier acuity is more precise than spatial-frequency discrimination over comparable ranges of feature separations, i.e. gap and spatial-frequency. This general observation that the precision of spatial displacement judgments is enhanced by the presence of multiple orientation cues, suggests that neural representations of spatial separations and orientations may be functionally combined for the computation of spatial discriminations. (Refs: C1b and C1e)

C2c. A two-dimensional surround provides a bisection advantage

We introduce a new spatial discrimination task where the observer discriminates offset from the geometric center of a circle. We find that the jnd for circle-center discrimination is lower than the jnd for comparable two-dot bisection discrimination tasks when the circle diameter and dot separtion is larger than some critical radius (approximately 0.50 - 0.66 degrees). This finding documents an advantage due to a two-dimensional stimulus and suggests that the visual system is able to exploit two-dimensional spatial parameters in order to achieve a spatial discrimination advantage. The advantage increases with circle radius and suggests the eye is able to exploit spatially integrated information to enhance accuracy in spatial discrimination. (Refs: C1g, manuscript in preparation)

C2d. Two-dot Vernier acuity falls within two degrees of the foveal center

Vernier acuity, Δv, as a function of two-dot separation, s, was masured at five retinal locations between the foveal center and 2.0 deg of retinal eccentricity. We find that the Vernier Weber fraction ($\Delta v/s$) increases by nearly a factor of 2 from the foveal center to 2.0 deg of retinal eccentricity. Comparison of these results with cone spacings at each of the corresponding retinal eccentricities indicates that the angular dot separations at which the Δv vs s function intersects the angular cone spacings at each eccentricity remain nearly constant. These results are consistent with a model of spatial discrimination where both receptor and postreceptor factors contribute to the limits of Vernier acuity with 2 deg of the foveal center. (Refs: C1c and C1h)

D. REPORT OF SPECIFIC AIM 3

D1. List of publications

D1a. Costaridou, L.; Stefanou, S.; Hirsch, J. and Orphanoudakis, S. Image reconstructions based on the human and monkey cone mosaics: Cone-positions-Known and cone-positions-ignored models of retinocortical mapping. Visual Communication and Image Representation, 1(1), In press, 1990.

D1b. Costaridou, L., Stefanou, S., Hirsch, J. and Orphanoudakis, S. Image reconstruction through the primate cone mosaic. Technical Report: RCC/CSI/TR/1989/017, Institute of Computer Science, Foundation of Research and Technology, Hellas, Greece, 1989.

D1c. Cher, D.J., Orphanoudakis, S. and Hirsch, J. Simulation of imaging, localization and spatial discrimination of dot stimuli based upon a simple model of retinocortical mapping and the human photoreceptor lattice. Yale Journal of Biologyand Medicine, 63, In press, 1990.

Dld. Hirsch, J., Orphanoudakis, S., Costaridou, L., and Stefanou, S. Simulation of image sampling and reconstruction based on actual human and monkey foveal cone mosaics confirms that the cone-positions-known (CPK) model is superior to the cone-positions-ignored (CPI) model. Supplement to Investigative Ophthalmology and Visual Science, 31, 414, 1990.

D2. Summary of main findings

D2a. Simulation of localization and spatial discrimination of dot stimuli based upon retinocortical mapping and the human photoreceptor lattice

The hypothesis of this study is that spatial sampling, localization and discrimination can be modeled based only upon the spatial geometry of the human photoreceptor lattice. We present a mathematical simulation of the sampling of simple stimuli by the human retinal photoreceptor lattice, the localization of these stimuli by the retinocortical apparatus, and the computation of spatial discrimination thresholds based upon the stimulus localization data. After a stimulus is sampled by the retinal lattice, an estimation of the true retinal location of the stimulus can be made by a weighted average method in which the position of each cone in the lattice is multiplied by the intensity of light stimulating the cone. The retinocortical scale produced by this method of stimulus localization is related to both photoreceptor density and disorder. We apply the data obtained from this method of retinal stimulus localization to a simulated spatial discrimination task similar to that which has been extensively investigated in human observers. Using the actual human photoreceptor lattice and ordered (perfect) lattices whose photoreceptor densities are matched to that of the human lattice, we calculate spatial discrimination indices or relative estimates of the limits of spatial discrimination as constrained by these lattices. By comparisons of the data generated by simulations using the actual and ordered sampling lattices, the effects of photoreceptor density and photoreceptor positional disorder can be isolated. Two methods of calculating spatial discrimination indices are presented. Method 1 calculates the "perceived" (i.e., simulated) difference in separation based upon a constant fractional actual deviation. Method 2 calculates that actual difference in separation based upon a constant central spatial discrimination criterion. Calculated dot locations using the ordered lattices fall along straight lines (passing through the origin of the "perceived" vs. applied location axes), and the slopes of the lines are related to the photoreceptor sizes. Calculated dot locations using the actual lattice deviate from the ordered controls progressively with increasing retinal eccentricity. This result suggests that lattice disorder (as well as spacing) influences the results of these simulations. According to Method 1, the human retinal lattice is less sensitive to small spatial deviations relative to density-matched ordered lattices. Similarly, Method 2, the inverse of Method 1, yields elevated spatial discrimination thresholds for the human lattice (i.e., predicted discrimination acuity is worse) relative to the density-matched ordered lattices. Both methods reflect precision losses due to photoreceptor spacing and disorder. (Refs: D1c, manuscript in preparation)

D2b. Simulation of image reconstruction based on human and monkey cone mosaics

We investigate the image reconstruction capacity of the actual foveal cone sampling mosaics of an adult monkey and human through computer simulations. A cone positions known retinocortical mapping model has been implemented, which makes use of classical Whittaker-Kotelnikov-Shannon, WKS, reconstruction theory and a two-dimensional hexagonal tessellation technique that maps the cone lattice onto a perfectly hexagonal grid. The cone-positions-known model is compared to a

cone-positions-ignored model model of retinocortical mapping. Comparisions of these two models of retinocortical mapping are based on the RMS error per pixel between the original and reconstructed images. Results of these simulations demonstrate a pronounced superiority of the CPK model vs the CPI model. The results of these simulations, which use "biologically correct" sampling lattices, document a potential image reconstruction advantage when cone positions are known. (Refs: D1a, D1b, and D1d)

E. REPORT ON STUDENTS AND APPLICATIONS

E1. Yale graduate students sponsored by PI

NAME	DEGREE	DATE	TITLE OF THESIS
Lisa Grohskopf	(MD)	current	Is the precision of human spatial discrimination influenced by the pattern of spatial elements?
Mark Bianchi	(MD)	current	Comparison of human and monkey peripheral photoreceptor sampling mosaics
Stacey Raymond	(MD)	current	Spatial complexity and the consequences for the precision of human vision
Spyros Stephanou	(PhD)	current	Simulations of human visual processing using representations of the biological sampling mosaic
Chander N. Samy	MD	1990	Comparisons of human and monkey retinal photoreceptor sampling mosaics
Daniel J. Cher	MD	1990	Simulation of imaging, localization and spatial discrimination of dot stimuli based upon a simple model of retinocortical mapping and the human photoreceptor lattice
Jack L. Gallant	PhD	1989	Mechanisms of spatial selective attention
Leslie M. Sims	MD	1989	Computerized automated perimetry: An assessment of visual field changes before and after focal photocoagulation for clinically significant diabetic macular edema
Michael Morris	MD	1989	Laser interferometric predictions of contrast sensitivity following IOL implantation
Zachary Klett	MD	1989	The correlation between objective lens opacity and laser interferometric contrast sensitivity in the cataract patient
Peggy Mei-Chi Liao	MD	1988	Correct loss variance can discriminate between control subjects and glaucoma suspect patients with no loss of visual sensitivity
Eric Jankelovits	MD	1987	The assessment of retinal function in cataract patients using laser interferometry
David B. Granet	MD	1987	Vernier acuity and motion: A comparison of athletes and non-athletes
Subba Gollamudi	MD	1987	An evaluation of corrected loss variance as a useful field index in glaucoma

E2. Publications of student research

Morris, M.; Klett, Z.; Gieser, S.C.; Couch, J.M. and Hirsch, J. Assessment of potential contrast sensitivity. Part I: Preoperative prediction of contrast sensitivity following IOL implantation. J. Cataract & Refract. Surg., In press, 1990.

Klett, Z.; Morris, M.; Gieser, S.C.; Couch, J.M. and Hirsch, J. Assessment of potential contrast sensitivity. Part II: The relationship between objective lens opacity and laser interferometric contrast sensitivity in the cataract patient. J. Cataract & Refract. Surg., In press, 1990.

Sims, L.M., Stoessel, K., Thompson, J.T. and Hirsch, J. An assessment of visual field changes before and after focal photocoagulation for clinically significant diabetic macular edema. Ophthalmologica, 200, 133-141, 1990.

Liao, P.M.; Gollamudi, S.R. and Hirsch, J. Evaluation of corrected loss variance as a field index: Part I. Corrected loss variance can discriminate between glaucoma suspect patients with no loss of visual sensitivity and control observers. Ophthalmologica, 197, 136-143, 1988.

Gollamudi, S.R.; Liao, P.M. and Hirsch, J. Evaluation of corrected loss variance as a field index: Part II. Corrected loss variance in conjunction with mean defect can identify stages of glaucoma. Ophthalmologica, 197, 144-150, 1988.

Jankelovits,E.R.; Lichtenstein,S.J.; Groll,S.L.; Remijan,P.W.; and Hirsch,J. Assessment of retinal function in cataract patients using laser interferometry to measure contrast sensitivity. Applied Optics, 27, 1057-1063, 1988.

Klett, Z., Gieser, S.C., Couch, J.M., Morris, M. and Hirsch, J. The correlation between lens opacity and loss of contrast sensitivity. Supplement to Investigative Ophthalmology and Visual Science, 30, 499, 1989.

Morris, M., Couch, J.M., Gieser, S.C., Klett, Z. and Hirsch, J. Laser interferometric predictions of contrast sensitivity following IOL implantation. Supplement to Investigative Ophthalmology and Visual Science, 30, 498, 1989.

Lebowitz, H.A., Thompson, J.T., Stoessel, K.M. and Hirsch, J Reduction in contrast sensitivity in the presence of simulated vitreous hemorrhage. Supplement to Investigative Ophthalmology and Visual Science, 30, 237, 1989.

Sims, L.M. and Hirsch, J. Computerized static perimetry: An assessment of visual field chnages before and after photocoagulation for clinically significant diabetic macular edema. Yale Journal of Biology and Medicine, 62, 317, 1989.

Morris, M.M. and Hirsch, J. Laser interferometric predictions of contrast sensitivity following IOL implantation. Yale Journal of Biology and Medicine, 62, 312, 1989.

Klett, Z.G. and Hirsch, J. The correlation between objective lens opacity and laser interferometric contrast sensitivity in the cataract patient. Yale Journal of Biology and Medicine, 62, 308, 1989.